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Push–pull training reduces foveal sensory eye dominance within the early visual channels

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ABSTRACT

A push–pull training protocol is applied to reduce sensory eye dominance in the foveal region. The training protocol consists of cueing the weak eye to force it to become dominant while the strong eye is suppressed when a pair of dichoptic orthogonal grating stimulus is subsequently presented to it (Ooi & He, 1999). We trained with four pairs of dichoptic orthogonal gratings (0°/90°, 90°/0°, 45°/135° and 135°/45° at 3 cpd) to affect the interocular inhibitory interaction tuned to the four trained orientations (0°, 45°, 90° and 135°). After a 10-day training session, we found a significant learning effect (reduced sensory eye dominance) at the trained orientations as well as at two other untrained orientations (22.5° and 67.5°). This suggests that the four pairs of oriented training stimuli are sufficient to produce a learning effect at any other orientation. The nearly complete transfer of the learning effect across orientation is attributed to the fact that the trained and untrained orientations are close enough to fall in the same orientation tuning function of the early visual cortical neurons (~37.5°). Applying the same notion of transfer of learning within the same feature channel, we also found a large transfer effect to an untrained spatial frequency (6 cpd), which is 1 octave higher than the trained spatial frequency (3 cpd). Furthermore, we found that stereopsis is improved, as is the competitive ability between the two eyes, after the push–pull training. Our data analysis suggests that these improvements are correlated with the reduced sensory eye dominance after the training, i.e., due to a more balanced interocular inhibition. We also found that the learning effect (reduced SED and stereo threshold) can be retained for more than a year after the termination of the push–pull training.

1. Introduction

Sensory eye dominance (SED) manifests as an unequal mutual inhibition between the two ocular channels (Ooi & He, 2001). SED can be revealed when two dissimilar dichoptic images with equal physical strength are presented to the observer to trigger the interocular inhibitory mechanism to suppress one of the two images. For observers with a significant SED, the image in the weak (non-dominant) eye is more frequently suppressed. Since equal mutual interocular inhibition is required for efficient processing of binocular information, a significant magnitude of SED can reduce stereo acuity and slow down stereo processing (Halpern & Blake, 1988; Kontsevich & Tyler, 1994; Legge & Gu, 1989; Ooi & He, 1996; Schor, 1991; Wolfe, 1986; Xu, He, & Ooi, 2010, in press). SED is not necessarily correlated with motor eye dominance, which is related to ocular dominance of perceived visual direction (Ooi & He, 2001).

Fig. 1 illustrates an example of two pairs of dichoptic test stimuli used to quantify SED. Here, in stimulus (a), the contrast of the vertical grating viewed by the right eye (RE) is fixed (constant) while the contrast of the horizontal grating viewed by the left eye (LE) is variable. During the test trial, the observer is presented with stimulus (a) for a brief interval (500 ms), and reports whether he/she sees a vertical or horizontal grating disc. Then using an adaptive procedure (QUEST), the contrast of the horizontal grating is appropriately adjusted according to the observer's report. The horizontal grating contrast is further adjusted after each subsequent trial until the observer experiences equal percentage of seeing the two gratings (point of equality). The contrast of the horizontal grating at this point of equality is referred to as the LE horizontal balance contrast. To obtain the RE horizontal balance contrast, the vertical and horizontal gratings are switched between the two eyes as in stimulus (b), and the contrast of the horizontal grating now in the RE is adjusted again until the point of equality is obtained. The difference between the LE and RE balance contrast values is defined as the SED.

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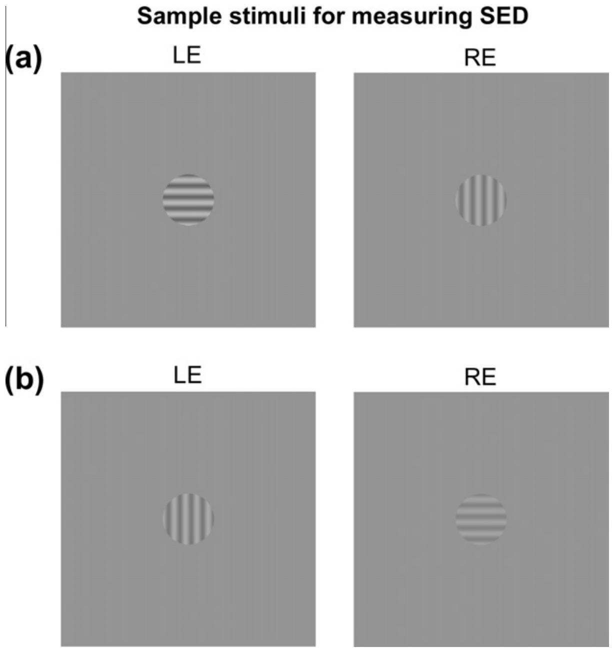

Fig. 1. Sample stimuli for measuring SED. (a) The LE balance contrast is obtained by varying the horizontal grating contrast while keeping the contrast of the vertical grating seen by the RE constant (1.5 log unit). The balance contrast is reached when the two eyes obtain an equal percentage of perceiving the two gratings (point of equality). (b) The gratings are switched between the two eyes to obtain the RE balance contrast of the horizontal grating. The difference between the LE and RE balance contrast values defines the SED.

Research on how to effectively reduce SED in adults – and thus improve binocular visual function – through visual training has important theoretical implications for neuroscience and vision research. For example, since the SED is a manifestation of an unbalanced interocular inhibitory mechanism, we can use it as a model to investigate adult neural plasticity of the inhibitory cortical network and its impact on behavior (Harauzov et al., 2010; Hensch et al., 1998; Huang et al., 1999; Karmarkar & Dan, 2006). Moreover, the clinical condition of amblyopia can be considered as an extreme case of SED, where the amblyopic eye receives an unbalanced amount of interocular inhibition. Consequently, reducing an amblyopic patient's SED can be an important part of the amblyopic therapy. We recently developed an approach to effectively reduce adult observers' SED using a perceptual learning protocol. Calling it the push–pull training protocol, we found that the push–pull protocol effectively reduces SED and enhances stereopsis of observers with otherwise clinically normal binocular vision (foveal stereo acuity $\leqslant$20 arcsec) (Xu et al., 2010).

Fig. 2a depicts the design of the push–pull training protocol. During each training trial, a square frame acting as an attention cue is presented to the weak eye to cause the dominance of the half-image (vertical grating) viewed by the weak eye (push) and the suppression of the half-image (horizontal grating) viewed by the strong eye (pull). Importantly, this strategy in the push–pull protocol is different from the more conventional "push-only" protocol (not shown), where only the weak eye is stimulated (push) with a visual image while the strong eye is not stimulated (no pull). Of significance, the extra "pull" component of the push–pull training protocol stimulates the strong eye while denying its retinal image from being perceived. This presumably reduces the strong eye's transmission efficiency and its effectiveness in suppressing the weak eye (Hebb, 1949; Xu et al., 2010), leading to reduced SED and improved stereopsis.

There are reasons to believe that the perceptual learning effect on SED with the push–pull training protocol is due to the plasticity of the primary visual cortex (V1). [The primary visual cortex as a potential site for plasticity has also been suggested by studies that investigated other aspects of perceptual learning (e.g., Fahle, 2004; Gilbert, Sigman, & Crist, 2001; Sagi & Tanne, 1994; Sasaki, Nanez, & Watanabe, 2010).] First, we observed that the reduction in SED is limited to the orientation of the stimulus (grating) used during training. A test grating orientation that is 45° away from the trained orientation elicits no change in SED after the training (Xu et al., 2010). This indicates that the perceptual learning is orientation specific, which has been considered a hallmark indicator of early cortical involvement (Fahle, 1997, 2004; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). Second, the perceptual learning effect (reduced SED and improved stereopsis) is only found at the trained retinal location (Xu et al., 2010), suggesting local neural plasticity. Third, the learning effect can be obtained without top-down attention modulation, suggesting the contribution of a stimulus-driven learning mechanism (Xu et al., in press). These findings are consistent with the spike response properties of V1 neurons, i.e., orientation selectivity with a narrow tuning function, relatively small receptive field sizes (local processing) and relatively weak top-down attention modulation (compared to neurons in the higher cortical levels) (Kastner & Ungerleider, 2000; McAdams & Maunsell, 1999; Yoshor, Ghose, Bosking, Sun, & Maunsell, 2007). Furthermore, the interocular inhibition and interactions of the signals between the two eyes (that results in SED) more likely occur in V1, where the majority of monocular neurons that carry the eye-of-origin information are found (Blake, Westendorf, & Overton, 1980; Maunsell & Van Essen, 1983; Ooi & He, 1999).

In the current report, we further reveal the impact of the learning effect on the binocular visual system with the push–pull training protocol by focusing on two issues. First, we investigated the learning effect in the foveal region. Up to now, we have only trained, and found, the learning effect in a parafoveal region (2° eccentricity). Clearly, we also need to explore whether a similar learning occurs in the foveal region since it has a prominent role in vision. We cannot simply assume that the learning should also occur in the foveal region, as perhaps, the adult visual cortex representing the peripheral retina might be more receptive to perceptual training than the foveal representation. This is because most task relevant visual information for our daily activity comes from the foveal region. In other words, the foveal representation having been overly exposed to an assortment of visual information could be less receptive to training, which requires repetitive exposures to similar information. Furthermore, even if the push–pull training protocol works in the foveal region, we need to explore if it is much more difficult to train the foveal region. This knowledge can also help us design a more efficient push–pull training protocol.

The second issue investigated in this report pertains to the generalization of the perceptual learning effect. As mentioned earlier, the primary visual cortex is probably the main site for the neural plasticity underlying the reduction in SED. Therefore, the impact of the push–pull training might be largely limited to the neurons, or neural networks (channels), tuned to the image properties of the training stimuli. However, since the ultimate goal of visual training is to reduce SED across all stimulus dimensions (properties), we have to generalize the learning effect to the neural channels whose optimal selectivity is beyond those of the training stimuli. For example, we have shown that the learning effect (reduced SED) with vertical/horizontal training stimuli does not transfer to the oblique (45°/135°) orientation (Xu et al., 2010). Consequently, to reduce SED across all orientation channels, we need to include additional training stimuli with other orientations.

How many discrete orientations do we need to train for the learning effect to benefit all orientation channels? In theory, four orientations with 45° separation in between (180°/4 = 45°) are

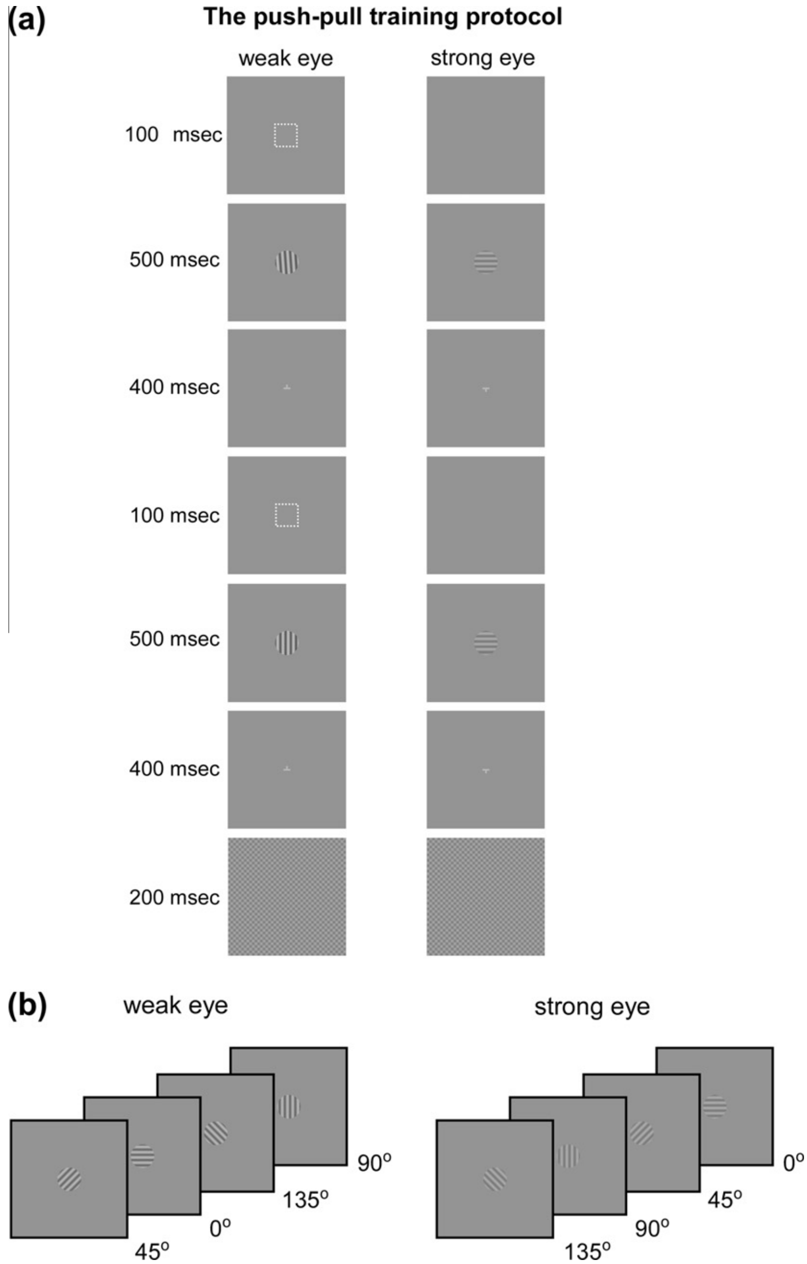

Fig. 2. (a) Stimulation sequence in the push–pull training protocol. A square frame is presented to the weak eye to cue attention to it, causing it to be dominant when the two eyes are subsequently stimulated with the binocular rivalry gratings. Four hundred milliseconds later, the same sequence of event is repeated but with the grating seen by the weak eye having a slightly different orientation from the first grating seen by the same eye. The observer reports whether the first or second vertical (or near-vertical) grating has a more counterclockwise orientation. (b) The four pairs of binocular rivalry gratings used for training (and also to measure SED). These gratings are randomly intermingled in the same training block of trials, so that the weak eye is stimulated with all four grating orientations (0°, 45°, 90° and 135°).

sufficient. This is because the estimated orientation bandwidth of the orientation tuning function of early cortical neurons is approximately 30–40° (Campbell & Kulikowski, 1966; De Valois, Albrecht, & Thorell, 1982; Hubel & Wiesel, 1968; McAdams & Maunsell, 1999; Movshon & Blakemore, 1973; Parker & Hawken, 1988; Phillips & Wilson, 1984). Fig. 3 illustrates an orientation tuning function of early cortical neurons modeled with a Gaussian distribution function centered at the 45° orientation with a standard deviation of 37.5° (McAdams & Maunsell, 1999). Clearly, cortical neurons with this tuning function will response with most spike activities to a 45° oriented grating stimulus. The response rate will reduce as the grating (with the same contrast level) is rotated away from the 45° orientation. Such a tuning function therefore predicts that the neural responses will be less when the grating is oriented at either 0° or 90°. Thus, if we train with 0° and 90° grating stimuli, we will be less likely to induce a significant learning effect in neurons with peak responses at 45° (Xu et al., 2010). However, we should still be able to induce a substantial learning effect in neurons optimally tuned to 22.5° and 67.5° (i.e., 45° ± 22.5°). Accordingly, we predict one only needs two pairs of orthogonal gratings as the training stimuli [i.e., 0°/90° and 45°/135°].

Nevertheless, the analysis above does not preclude the speculation that training with 0° and 90° grating stimuli might also induce a learning effect on neurons with an optimal orientation tuning at 45°. This is because these neurons can still be activated by the 0° and 90° grating stimuli, though with much reduced spike activities (see Fig. 3). Perhaps, one could compensate for the reduced activities by increasing the intensity (dosage) of the training such as with higher contrast, longer training hour/session and selective

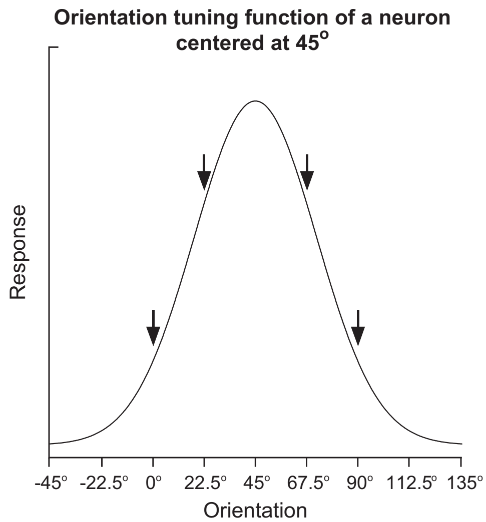

Fig. 3. The orientation tuning function of early cortical neurons modeled with a Gaussian distribution function centered at the 45° orientation with a standard deviation of 37.5°. Cortical neurons with such a tuning function respond much less to the 0° and 90° grating stimuli than to the 22.5° and 67.5° grating stimuli (arrows).

attention effort. Incidentally, we previously observed a small, but significant learning effect for a test stimulus that is orthogonal to the training stimulus only when observers selectively attended to the training stimulus (Fig. 2 in Xu et al., in press). However, this speculation requires further empirical investigations, which are beyond the scope of the present study.

In this paper, we tested and found a complete transfer of the learning effect to the untrained orientations (22.5° and 67.5°) with two pairs of training stimuli (0°/90° and 45°/135°). In addition, we investigated whether the learning effect is transferable to an untrained spatial frequency within the bandwidth of the tuning function (1 octave), and to other untrained stimulus contrast levels (±0.2 log unit from the trained grating contrast).

2. Methods

2.1. Basic experimental design

The push–pull training (Fig. 2a) was implemented over 10 days (1 session/day). During the training, the foveal location was stimulated with four dichoptic pairs of orthogonal grating discs (1.5°) (Fig. 2b) using four interleaved QUEST procedures in a random order. This allowed us to train four orientations: 0°, 45°, 90° and 135°. To assess the learning effect, measurements of SED, binocular rivalry and stereopsis were made before and after the training phase. For the SED test, we measured SED with the trained stimulus specifications [orientations (0°, 45°, 90° and 135°), contrast (1.5 log unit), spatial frequency (3 cpd)], untrained contrast levels (1.3 and 1.7 log unit), untrained orientations (22.5° and 67.5°), and untrained spatial frequency (6 cpd). For the binocular rivalry test, we measured the dynamics of interocular dominance and suppression over an extended (30 s) viewing period with horizontal and vertical dichoptic gratings. For the stereopsis test, we measured the stereo threshold with a random-dot stereogram.

2.2. Observers

Eight naïve observers (23–33 years old) with informed consent and clinically normal binocular vision participated in the study. They had normal, or corrected to normal, visual acuity in each eye (at least 20/20), stereoacuity of ⩽40 arcsec and fixation disparity of ⩽8.6 arcmin. During the experiments, they viewed the computer monitor through a haploscopic mirror system attached to a head-and-chin rest from a distance of 85 cm.

2.3. Stimuli and procedures

A MacPro computer running Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) generated the stimuli that were displayed on a 21-in. Samsung SyncMaster flat screen CRT monitor. The monitor's resolution was set to 1280 × 1024 pixels at 100 Hz refresh rate for all experiments, except for the stereo threshold experiment (2048 × 1536 pixels at 60 Hz).

2.3.1. Measuring foveal SED

2.3.1.1. SED at the trained stimulus orientation. (i) *In the pre- and post-training test phases*: We measured, in a random order, SED at four orientations (0°, 45°, 90° and 135°) using the four pairs of binocular rivalry stimuli [2 eyes (left and right) × 2 orientation pairs (0°/90° and 45°/135°)] shown in Fig. 2b. (These same stimuli were also used for the push–pull training.) To prepare for a SED test trial, the observer aligned his/her eyes by fixating centrally on a nonius target (0.45° × 0.45°, line width = 0.1°, 52.5 cd/m^2). He/she then pressed the spacebar on the computer keyboard to remove the nonius target. This was followed by the presentation of the dichoptic orthogonal grating discs (500 ms), and a 200 ms mask (7.5° × 7.5° checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2, 1.5 log unit contrast) to terminate the trial. The observer responded to his/her percept, 0° or 90° for the 0°/90° grating stimulus, or 45° or 135° for the 45°/135° grating stimulus, by pressing the appropriate key. If he/she saw a mixture of the two gratings, he/she would respond to the predominant orientation perceived. A QUEST procedure was used to adjust the grating contrast in one half-image according to the observer's response (the grating contrast in the other half-image was kept constant at 1.5 log unit). By appropriately adjusting the grating contrast after each trial, the point of equality, where the observer obtained an equal chance of seeing the two gratings (equal predominance) was reached. The obtained contrast is the balance contrast for the eye that viewed the variable contrast grating. We then switched the gratings between the two eyes, to obtain the mean balance contrast for the fellow eye. Two such blocks of trials (50 trials/block) were run to obtain the mean balance contrast for each eye. The difference between the LE and RE mean balance contrast values is defined as the SED. For convention and ease of referencing, if we adjusted the contrast of the 0° (horizontal) grating of the 0°/90° grating stimulus, the obtained SED is labeled as 0–0°/90° SED. (That is, the first number is the orientation of the grating with the variable contrast while the second and third numbers indicate the orientations of the dichoptic grating stimulus used in the SED test.)

(ii) *During the training phase*: We measured the 0–0°/90° SED and 45–45°/135° SED before and after each even day's training session. Meanwhile, the 90–0°/90° SED and 135–45°/135° SED were measured before and after each odd day's training session.

2.3.1.2. SED with an untrained stimulus property in the pre- and post-training phases. To investigate whether the learning effect (reduced SED) is transferable, we measured SED with binocular rivalry stimuli whose spatial properties were the same as the training stimuli in all aspects except one (contrast, orientation or spatial frequency). Specifically, we tested:

i. 0–0°/90° SED and 45–45°/135° SED at two different fixed contrast levels: 1.3 log and 1.7 log units. (Recall that our standard SED test stimulus had the grating of one half-image with a variable contrast level, while the contrast of the grating in the other half-image was kept constant at 1.5 log unit. The training was also carried out with one half-image of the training stimulus having a contrast level of 1.5 log unit.)

ii. 22.5–22.5°/112.5° SED and 67.5–67.5°/157.5° SED, i.e., 22.5° away from the trained orientations.

iii. 0–0°/90° SED and 45–45°/135° SED at 6 cpd, i.e., 1 octave higher than the trained spatial frequency (3 cpd).

2.3.2. The push–pull training protocol stimulating the foveal region

To begin a training trial, the observer aligned his/her eyes at the nonius fixation target (0.45° × 0.45°, line width = 0.1°, 52.5 cd/m^2), and then pressed the spacebar on the computer keyboard. This led to the removal of the nonius fixation target, which was replaced by the presentation of a monocular square frame (1.5° × 1.5° frame with dash outline, width = 0.1°, 1.52 log unit, 70 cd/m^2) in the weak eye for 100 ms (Fig. 2a). The square frame acted as a transient attention cue to attract attention to the vicinity of the cue in the weak eye (Ooi & He, 1999). After a 100 ms cue-lead-time, a pair of dichoptic orthogonal gratings (500 ms, 1.5°, 3 cpd, 35 cd/m^2) was presented. The same 100 ms cue was presented again 400 ms later, followed by a 100 ms cue-lead-time, and the presentation of a second pair of dichoptic gratings (500 ms). The grating orientation shown to the weak eye in this second presentation had a slightly different orientation from the grating shown in the first presentation. Four hundred msec after the dichoptic grating presentation a binocular checkerboard sinusoidal grating mask (200 ms, 7.5° × 7.5°, 3 cpd, 35 cd/m^2, 1.5 log unit contrast) was presented to terminate the trial. The contrast values of the dichoptic gratings used in the training were those that led to the points of equality in the RE and LE with the SED test obtained before the training phase. The observer's (orientation discrimination) task was to report by key press whether the first or second grating had a slight counterclockwise orientation, and an audio feedback was given. This ended a training trial.

Five hundred training trials were run during each day's training session. These trials were blocked into 100 trials/block, i.e., five blocks of trials were performed on each training day. Within each block of trials, four pairs of dichoptic training stimuli (Fig. 2b) were presented to the observer to train the weak eye at four different orientations (0°, 45°, 90°, and 135°). Trials with the four different orientations (25 trials per orientation) were intermingled and their order of presentation was randomized. Thus, to determine the orientation discrimination threshold for each stimulus orientation, four randomly interleaved QUEST procedures were run during each block of 100 trials. Before commencing the proper training phase, we ascertained for each observer that the cue successfully suppressed the grating viewed by the strong eye.

2.3.3. Dynamics of interocular dominance and suppression

The stimulus was the same as the 0°/90° binocular rivalry stimulus used to measure SED, except for the stimulus presentation duration. Specifically, it comprised a pair of dichoptic vertical and horizontal grating discs (1.5°, 3 cpd, 35 cd/m^2, 1.5 log unit contrast) surrounded by a 7.5° × 7.5° gray square (35 cd/m^2). To begin a trial, the observer aligned his/her eyes on the nonius fixation target (0.45° × 0.45°, line width = 0.1°, 52.5 cd/m^2), and then pressed the spacebar on the computer keyboard. This led to the removal of the nonius fixation target, which was replaced by the presentation of the binocular rivalry gratings for 30 s. At the end of the 30 s, a 1 s mask (7.5° × 7.5° checkerboard sinusoidal grating, 3 cpd, 35 cd/m^2, 1.5 log unit contrast) terminated the trial. The observer's task was to report (track) his/her instantaneous percept of the binocular rivalry stimulus over the 30 s stimulus presentation duration. Depending on the percept, vertical, horizontal, or a mixture of both, he/she would depress the appropriate key until the next percept took over. The predominance, average duration and frequency of seeing these percepts were calculated. Two orientation-eye conditions (horizontal in weak eye and horizontal in strong eye) were run five times each in a randomized order.

2.3.4. Stereo threshold

A 7.5° × 7.5° random-dot stereogram (dot size = 0.0132°, 35 cd/m^2) with a variable crossed-disparity disc target (1.5°) was used (Fig. 9a). The Michelson contrast of the stereogram was individually selected for the observer, to make the stereo task moderately difficult and to avoid a possible ceiling-effect due to pixel-size limitation (0.8 arcmin). With this criterion, the contrast levels were set at 1.0 log unit for two observers, 1.1 log unit for two observers, 1.2 log unit for two other observers, and 1.3 and 1.5 log unit, respectively, for the remaining two observers.

We used the standard 2AFC method in combination with the staircase procedure to measure the stereo disparity threshold. The temporal sequence of the stimulus presentation was interval-1 (200 ms), blank (400 ms), interval-2 (200 ms), blank (400 ms), and random-dot mask (200 ms, 7.5° × 7.5°, 35 cd/m^2). The observer indicated whether the crossed-disparity disc was perceived at interval-1 or -2, and an audio feedback was given. Each block comprised 10 reversals (step size = 0.8 arcmin, total ∼50–60 trials), and the last eight reversals were taken as the average threshold. Each block was repeated four times and measured over 2 days.

To investigate whether the push–pull training has a long-term effect on stereo threshold, we tested all, but one observer, about 10 months or beyond after the termination of the training phase. One observer (whose stereo test contrast level was set at 1.1 log unit) had relocated and was not able to return to the laboratory. The remaining observers were able to return to the laboratory for a one-time testing, though not on the same day. Specifically, the remaining seven observers were tested on the 314th, 318th, 381st, 402nd, 459th, 470th, or 492nd day after the training phase terminated.

3. Results

3.1. Reduction in SED measured with stimuli similar to the trained stimuli

Fig. 4 depicts the average SED (0–0°/90°; 90–0°/90°; 45–45°/135°; 135–45°/135°) as a function of training session, measured using SED test stimuli with the same spatial properties as the four pairs of training stimuli (Fig. 2b). The open and filled symbols, respectively, represent the average SED measured before and after each day's training session. For all four stimuli, the SED is smaller before than after the training session [0–0°/90°: $F(1,7) = 22.061$, $p = 0.002$; 90–0°/90°: $F(1,7) = 17.797$, $p = 0.004$; 45–45°/135°: $F(1,7) = 27.981$, $p = 0.001$; 135–45°/135°: $F(1,7) = 25.408$, $p = 0.001$; 2-way ANOVA with repeated measures]. The trend of this finding (within-session increase in SED) is similar to those we found in the parafoveal region (Xu et al., 2010) and those found previously for other aspects of perceptual learning (Mednick, Arman, & Boynton, 2005; Mednick et al., 2002; Ofen, Moran, & Sagi, 2007; Yotsumoto, Chang, Watanabe, & Sasaki, 2009). We were able to monitor this (short-term) within-session increase in SED on three observers. We tested their SED over an hour after the training session ended for the day. We found the short-term increase in SED decays slowly (e.g., the effect can still be observed 30 min after the training session ended), suggesting the possible contributions of cortical contrast adaptation (Greenlee, Georgeson, Magnussen, & Harris, 1991), fatigue of the interocular inhibitory network, and/or general cognitive fatigue. Please refer to Section 3.7 for further discussion.

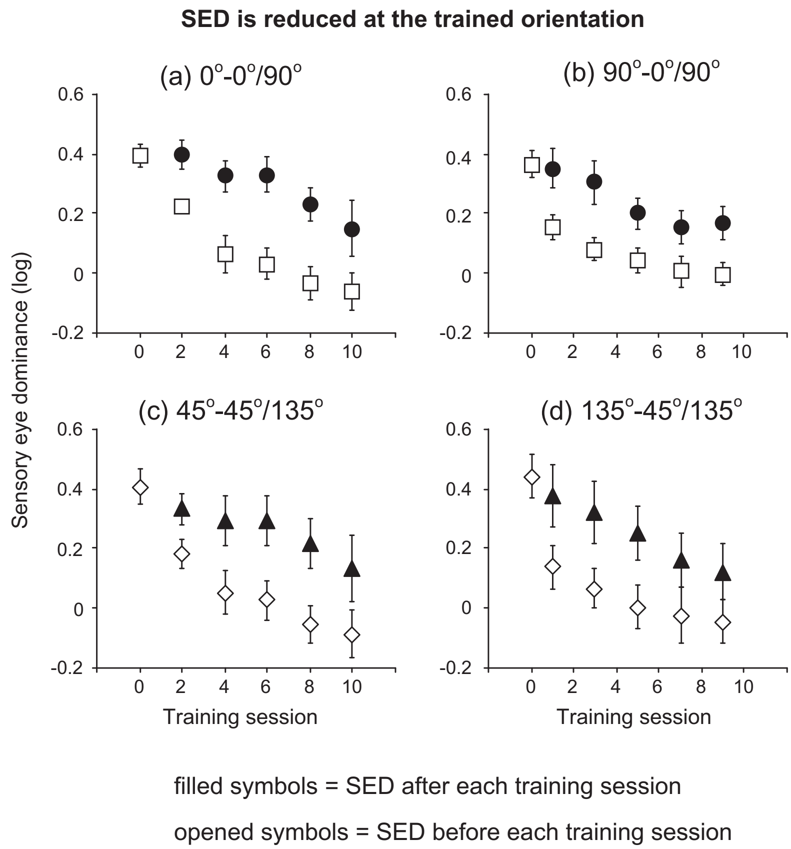

Fig. 4. (a–d) Results showing that SED is reduced at the trained orientations (0°, 90° 45° and 135°). The notation above each graph, e.g., 0–0°/90° in graph (a), indicates that to obtain the SED (as in Fig. 1), we adjusted the contrast of the 0° (horizontal) grating of the 0°/90° binocular rivalry grating stimulus. That is, the first number is the orientation of the variable contrast grating while the second and third numbers are the orientations of the dichoptic grating test stimulus. Generally, SED reduces as the training progresses. However, within each day's training session, SED is smaller before the training than after the training.

Importantly, the SED reduces gradually as the training progresses when it was measured either before (0–0°/90°: slope = −0.044, $R^2 = 0.898$, $p = 0.004$; 90–0°/90°: slope = −0.033, $R^2 = 0.803$, $p = 0.016$; 45–45°/135°: slope = −0.046, $R^2 = 0.881$, $p = 0.006$; 135–45°/135°: slope = −0.042, $R^2 = 0.768$, $p = 0.022$), or after each day's training session (0–0°/90°: slope = −0.030, $R^2 = 0.928$, $p = 0.008$, 90–0°/90°: slope = −0.025, $R^2 = 0.865$, $p = 0.022$; 45–45°/135°: slope = −0.024, $R^2 = 0.902$, $p = 0.013$; 135–45°/135°: slope = −0.033, $R^2 = 0.989$, $p = 0.001$). These observations thus demonstrate that the push–pull training protocol can significantly reduce SED in the foveal region, as in the parafoveal region.

3.2. Reduction in SED measured with an untrained stimulus property: Different fixed contrast level

So far, the measured SED had a fixed grating contrast of 1.5 log unit in one half-image, which was the same as the fixed contrast level used in one half-image of the training stimulus. To investigate whether the learning effect occurs for a test stimulus contrast level different from that of the trained stimulus contrast level, we measured 0–0°/90° SED and 45–45°/135° SED with either a higher (1.7 log unit) or lower (1.3 log unit) fixed contrast level than that used in the training stimulus (1.5 log unit). The graph in Fig. 5a shows that the average 0–0°/90° SED is significantly reduced after the training phase, when measured with either the lower and higher fixed contrast grating [1.3 log unit: $t(7) = 5.876$, $p = 0.001$; 1.7 log unit: $t(5) = 7.497$, $p = 0.001$]. [Note: Even though we trained eight observers, two observers could not be tested with the 1.7 log unit fixed contrast for the 0–0°/90° SED before the training (due to excessive SED) because the highest contrast level in the weak eye (∼2 log unit) could not balance out the fixed 1.7 log unit contrast in the strong eye. Therefore, we only included six observers' data when averaging the 0–0°/90° SED results.] The reduction in SED is similar at all three fixed contrast levels for all six observers tested [interaction effect between contrast level and session: $F(2, 10) = 1.257$, $p = 0.326$, 2-way ANOVA with repeated measures]. A similar learning effect is revealed for the 45–45°/135° SED [1.3 log unit: $t(7) = 9.680$, $p < 0.001$; 1.7 log unit: $t(7) = 7.386$, $p < 0.001$] (Fig. 5b). The reduction in SED is also similar for all three fixed contrast levels tested [interaction effect between contrast level and session: $F(2, 14) = 2.856$, $p = 0.091$, 2-way ANOVA with repeated measures].

3.3. Reduction in SED measured with an untrained stimulus property: different orientation

We measured 22.5–22.5°/112.5° SED and 67.5–67.5°/157.5° SED, whose orientations are 22.5° away from the nearest trained orientation (Fig. 6). A significant reduction in the average SED is found after the training phase [22.5–22.5°/112.5°: $t(7) = 5.802$, $p = 0.001$; 67.5–67.5°/157.5°: $t(7) = 9.160$, $p < 0.001$], indicating a transfer of perceptual learning to the untrained orientations. To quantify the transfer effect from all four trained orientations, we calculated a *transfer factor*. This is defined as the ratio of the mean reduction in SED from the two untrained orientation conditions (22.5–22.5°/112.5° and 67.5–67.5°/157.5°) to the mean reduction in SED from all four trained orientations (see "Mean trained" in the graph). We found the transfer factor to be 99.63%. This suggests an almost complete transfer of the learning effect to the untrained orientations, when the untrained orientations are within the

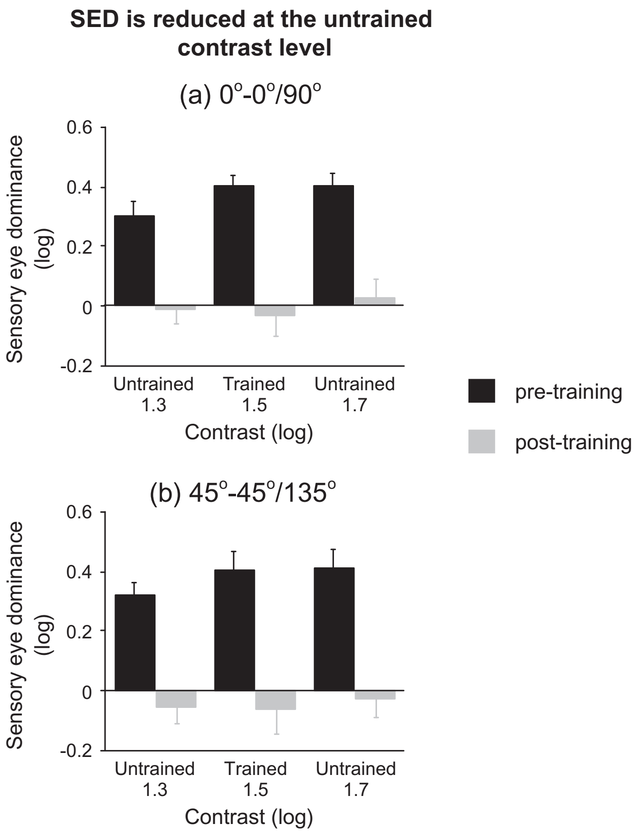

Fig. 5. (a and b) Results showing that SED is reduced at the untrained contrast levels (1.3 and 1.7 log units) with the 0–0°/90° and 45–45°/135° grating stimuli after the training phase. Training was performed with a fixed contrast level of 1.5 log unit in one half-image.

estimated bandwidth of the orientation tuning functions of the early visual cortex (Campbell & Kulikowski, 1966; McAdams & Maunsell, 1999; Movshon & Blakemore, 1973; Parker & Hawken, 1988; Phillips & Wilson, 1984). Furthermore, since the untrained orientations fall in the mid-ranges of the two trained orientations, which are 45° apart, our results indicate that the four orientations of the training stimuli (0°, 45°, 90° and 135°) can produce a similar learning effect at any other untrained orientation.

3.4. Reduction in SED measured with an untrained stimulus property: different spatial frequency

We measured 0–0°/90° SED and 45–45°/135° SED using test stimuli with 6 cpd, instead of 3 cpd (trained spatial frequency). The untrained spatial frequency of 6 cpd is one octave higher than the trained grating's and is within the estimated bandwidth of the spatial frequency tuning function centered at 3 cpd (Graham & Nachmias, 1971; Wilson, McFarlane, & Phillips, 1983). As shown in Fig. 7, the 0–0°/90° SED and 45–45°/135° SED were significantly reduced after the training [0–0°/90°: $t(7) = 3.311$, $p = 0.013$; 45–45°/135°: $t(7) = 2.661$, $p = 0.032$], indicating a transfer effect of perceptual learning to a different spatial frequency that is within the bandwidth of the same spatial frequency tuning function. We then calculated the SED transfer factors from the trained to the untrained spatial frequency (ratio between the reduced SED at 6 cpd and reduced SED at 3 cpd). We found relatively large transfer factors for both the 0–0°/90° (77.04%) and 45–45°/135° (70.77%) stimuli.

3.5. Significant learning effect on the dynamics of interocular dominance and suppression

We measured observers' performance in tracking their percepts (horizontal grating, vertical grating or mixture) while viewing a pair of dichoptic horizontal/vertical rivalry gratings for 30 s. There were two test conditions, one with the weak eye viewing the vertical grating and the other with the weak eye viewing the horizontal grating. For each test condition, we calculated the predominance, dominance duration, suppression duration, and dominance frequency for seeing horizontal and vertical gratings. We then calculated the performance ratio between the strong eye (SE) and weak eye (WE) to quantify the binocular rivalry percept for each measure. In the case of predominance, for example, the performance ratio is obtained by the formula:

$$\frac{[\text{Predominance (SE seeing vertical)} + \text{Predominance (SE seeing horizontal)}]}{[\text{Predominance (WE seeing vertical)} + \text{Predominance (WE seeing horizontal)}]} \quad (1)$$

Fig. 8 depicts the average performance ratio results for the various measures of the binocular rivalry percepts. A performance ratio of larger than unity indicates an imbalance that favors the

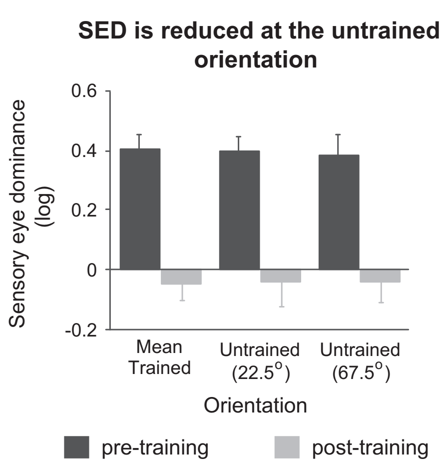

Fig. 6. Results showing that SED is reduced at the untrained orientations (22.5° and 67.5°). The mean trained data represents the average SED from all four trained orientations (0°, 45°, 90° and 135°).

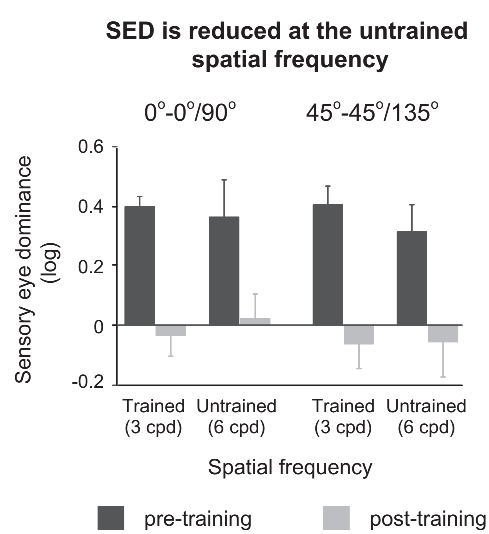

Fig. 7. Results showing that SED is reduced at the untrained spatial frequency (6 cpd) with the 0–0°/90° and 45–45°/135° grating stimuli. Training was performed with a fixed spatial frequency of 3 cpd.

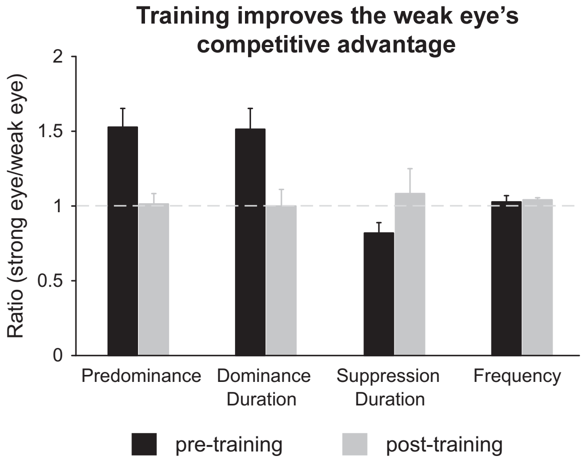

Fig. 8. Results showing that training improves the weak eye's competitive advantage during extended viewing of a (0°/90°) binocular rivalry stimulus. A performance ratio of larger than unity indicates an imbalance that favors the strong eye, and a performance ratio of unity indicates the two eyes are balanced. Clearly, all average performance ratios, except for the frequency performance ratio, change toward the balance level (dash line) after the training.

strong eye and a performance ratio of unity indicates the two eyes are balanced. Clearly, all average performance ratios, except for the dominance frequency performance ratio, change significantly toward the balance level (ratio = 1) after the training. Predominance: $t(7) = 7.073$, $p < 0.001$; Dominance duration: $t(7) = 9.339$, $p < 0.001$; Suppression duration: $t(7) = -2.406$, $p = 0.047$; Dominance frequency: $t(7) = -0.250$, $p = 0.810$. Additionally, we analyzed the mixture (piecemeal) percept but did not find a significant learning effect ($p > 0.250$).

As noted, other than the viewing duration, we used the same stimuli for measuring SED and the current binocular rivalry tracking test. The viewing duration for the SED test was 500 ms, which required the observers to quickly detect the appearance of the image seen. On the other hand, the viewing duration of the rivalry tracking task was 30 s, which allowed the observers ample time to experience the alternation of their percepts between dominance and suppression. Nevertheless, despite the difference, both psychophysical tasks provide insights into the behaviors of the interocular inhibitory mechanism. Measuring SED reveals the interocular imbalance at the initial stage of interocular inhibition, while tracking the binocular rivalry percept largely reveals the interocular imbalance between the eyes as they compete to maintain dominance and emerge from suppression. Consequently, we predict that the two measures should be correlated such that the same eye would have the competitive advantage in both tasks. By extension, the learning effect should be evident in (translate to) both tasks. We have confirmed this prediction in a correlation analysis that is elaborated in Section 4.

3.6. Significant learning effect on stereopsis: reduction in stereo threshold

We measured stereo depth thresholds with a random-dot stereogram and found a significant threshold reduction after the training phase [$t(7) = 11.325$, $p < 0.001$] (Fig. 9). This finding is similar to those found after training the parafoveal region in our previous study (Xu et al., 2010). Given that our observers were not exposed to the random-dot stereogram stimulus during the training phase, the observed learning effect on stereo depth perception also suggests that the push–pull training protocol modifies the binocular neural circuitries in the early cortical level. This could explain how a binocular perception (stereopsis) that is unrelated to the training stimulus, or task, improves.

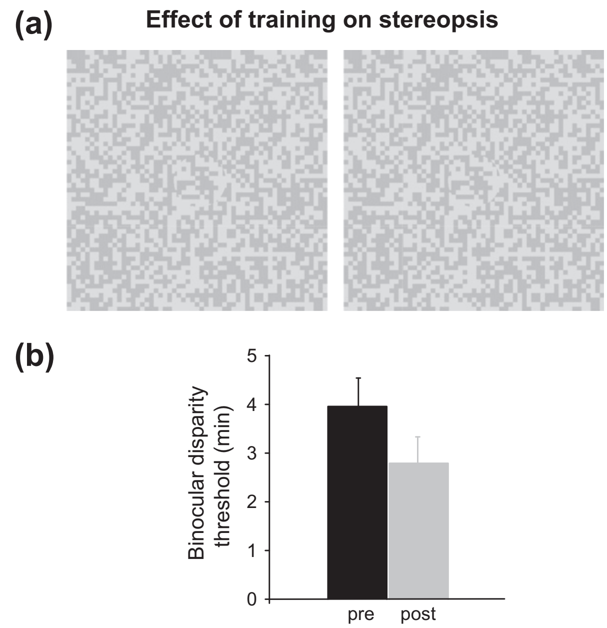

Fig. 9. (a) The random-dot stereogram used to measure stereo threshold. (b) Binocular disparity threshold is reduced after the training, even though the observers were never exposed to the stimulus, or task, during the training phase.

Additionally, we tested seven of the eight observers' stereo depth thresholds more than 10 months after the push–pull training phase ended to investigate the retention of the stereo learning effect. We found these observers exhibited an average stereo threshold of 2.99 ± 0.31 min. Importantly, the stereo threshold level (2.99 ± 0.31 min) is comparable with the average stereo threshold obtained immediately after the push–pull training phase ended [2.93 ± 0.61 min, $t(6) = 0.096$, $p = 0.926$]. Each observer's stereo depth threshold is smaller than the one measured before the start of the push–pull training phase, and on average the former is moderately smaller than the latter [4.17 ± 0.60 min; $t(6) = 2.064$, $p = 0.085$]. This suggests that the learning effect on stereopsis is retained for a relatively long period of time.

3.7. Reductions in the weak eye's orientation discrimination thresholds during the training phase

The observers' task during the push–pull training trials was to perform orientation discrimination of the gratings viewed by the weak eye. Essentially, while our goal was to reduce SED through training, orientation discrimination ability was also trained at four orientations (0°, 45°, 90° and 135°). To assess the training effect of orientation, we averaged the orientation discrimination thresholds from the five blocks of trials ran for each orientation during each training day (session). These are shown in Fig. 10a as a function of training session. There is a significant learning effect for all four orientations [0°: $F(9,36) = 2.829$, $p = 0.007$; 45°: $F(9,36) = 5.191$, $p < 0.001$; 90°: $F(9,36) = 6.085$, $p < 0.001$; 135°: $F(9,36) = 9.144$, $p < 0.001$, one-way ANOVA with repeated measures]. This finding is consistent with those found by others in perceptual learning studies of orientation discrimination (Appelle, 1972; Fahle, 1997; Fiorentini & Berardi, 1980; Sally, Poirier, & Gurnsey, 2005; Vandenbussche, Vogels, & Orban, 1986; Xiao et al., 2008; Zhang, Xiao, Klein, Levi, & Yu, 2010). However, it is notable that the orientation discrimination thresholds (~6°) for the oblique gratings found here are moderately higher compared to those typically reported in the literature (e.g., Tibber, Guedes, & Shepherd, 2006; Xiao et al., 2008; Zhang et al., 2010). Whether the elevated orientation discrimina-

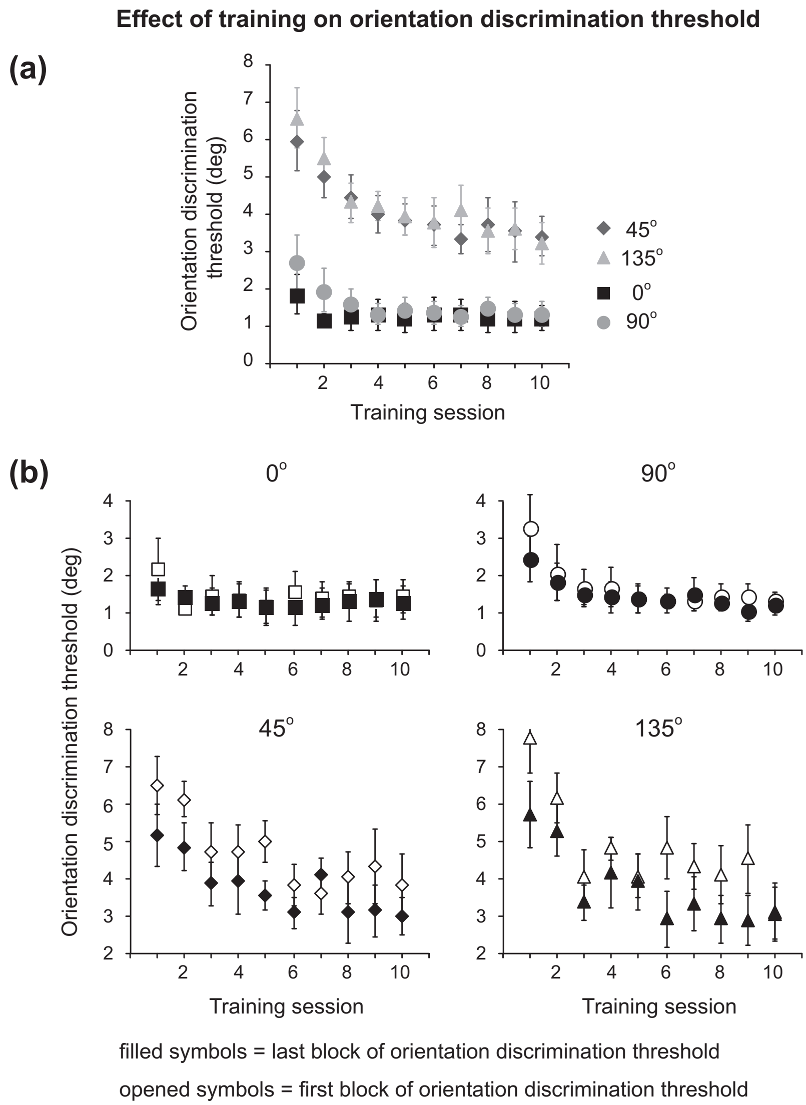

Fig. 10. The effect of training on the orientation discrimination thresholds during the training phase. (a) The change in the average orientation discrimination threshold as a function of training session for the four trained orientations (0°, 90° 45° and 135°). Each data point represents the average of the five blocks of training trials performed during each training session. For all orientations, thresholds decrease with training. (b) Each graph plots the average orientation discrimination thresholds for one orientation, from the first and last blocks of the training session (day). There is no significant difference between the first and last blocks of orientation discrimination thresholds with the 0° and 90° stimuli. However, with the 45° and 135° orientation discrimination thresholds, performance is better in the last block of training trials than the first block. Notably, this trend is opposite to the performance in SED shown in Fig. 4.

tion thresholds are related to the binocular rivalry condition inherent in the push–pull paradigm requires further investigations (previous studies did not use rivaling gratings).

Since five blocks of training trials were ran during each training session, we also compared the orientation discrimination thresholds between the first and the last blocks of the session. This allows us to reveal the behavior of the learning process within each day's training session. The average results of the four orientations are depicted in Fig. 10b (first block: open symbol; last block: filled symbol). There is no significant difference in orientation discrimination thresholds between the first and last blocks for the horizontal and vertical orientations [0°: $F(1, 7) = 1.525$, $p = 0.257$; 90°: $F(1, 7) = 2.060$, $p = 0.194$; 2-way ANOVA with repeated measures]. However, there exists a significant difference in orientation discrimination thresholds between the first and last blocks for the oblique orientations [45°: $F(1, 7) = 46.615$, $p < 0.001$; 135°: $F(1, 7) = 22.690$, $p = 0.002$, 2-way ANOVA with repeated measures]. Interestingly, the improved performance in orientation discrimination within the day's training for the oblique orientations is opposite to the trend found in the SED measures. In the latter, SED is smaller (improved) before than after the end of the training session (Fig. 2, also see Xu et al. (2010) with parafoveal data). Taken together, this suggests that the change in SED (i.e., the short-term, within-session increase in SED) cannot solely be explained by a general fatigue effect that degrades all types of perceptual performance.

We offer two possible explanations for the within-session increase in SED. First, as mentioned earlier, it could be caused by contrast adaptation in the early visual cortex (Blake & Fox, 1974; Blake, Tadin, Sobel, Raissian, & Chong, 2006; Blakemore & Campbell, 1969; Gardner et al., 2005; Greenlee et al., 1991; Movshon & Lennie, 1979; Ohzawa, Sclar, & Freeman, 1982; Truchard, Ohzawa, & Freeman, 2000). Specifically, the induced contrast adaptation during the training session (500 trials lasting about 1 h) could be larger for the training grating presented to the weak eye than for the training grating presented to the strong eye. This is because the dominant grating (seen by the weak eye) is more susceptible to contrast adaptation than the suppressed grating (seen by the strong eye) (Blake et al., 2006; Greenlee et al., 1991). Therefore, when SED is measured immediately after the training session, the weak eye's monocular channel being differentially more adapted would be disadvantaged. This is revealed as an increase in (within-session) SED.

However, the above monocular contrast adaptation explanation might not be the sole factor. We refer to our previous findings in a related study (Xu et al., 2010) where we trained two parafoveal regions, respectively, with the push–pull and push-only paradigms. (The push-only paradigm does not present a grating to the strong eye during the training, i.e., the strong eye channel does not undergo contrast adaptation.) We found increases in within-session SED at both locations, with the within-session SED increase being larger at the push–pull training location. Now, should monocular contrast adaptation be the sole factor, the within-session SED increase should instead be larger at the push-only training location. This is because the push-only training does not lead to an adaptation of the monocular strong eye channel since a grating is not presented to it during the training phase.

Consequently, we offer a second possible explanation for the within-session increase in SED. We speculate that subjecting the strong eye to multiple and consecutive interocular inhibition by the weak eye during the hour long push–pull training phase leads to a fatigue in the underlying interocular inhibitory network. This, effectively, causes the short-term shift in the balance point of mutual interocular inhibition toward the strong eye. Hence, the within-session SED is increased.

4. Discussion

The current study reveals that the push–pull training protocol can significantly reduce SED and improve binocularity in the foveal region. It extends our previous findings in the parafoveal region (Xu et al., 2010). A general comparison between the current Figs. 4 and 3c in Xu et al. (2010) suggests that the perceptual learning probably occurs at similar speeds in both retinal regions. Of course, a direct comparison between the exact speeds of perceptual learning in the two studies is not possible due to specific differences between the current training stimuli and procedures and those of Xu et al. (2010). For example, the current study trained with four orientation pairs and 125 training trials/orientation pair/day, whereas the previous study trained with one orientation pair and 600 training trials/orientation pair/day. Nevertheless, the agreement between the general comparison helps dispel our initial concern that the 500–600 push–pull training trials during each day's training session in the laboratory might not be sufficient to produce a meaningful impact on the foveal binocular visual system. This is because outside the laboratory training session, human observers frequently and attentively process an abundance of visual information with the fovea for the purpose of object recognition and visually guided action tasks, than with the peripheral retina. Accordingly, the heavy demands on the fovea for accomplishing everyday visual activities could have diluted the impact of the relatively brief laboratory training session.

We also reveal that the learning effect (reduced SED) is transferable to other untrained spatial image properties (contrast, orientation and spatial frequency). Pertaining to orientation, our finding suggests that four training gratings with 45° separation in orientation are sufficient to affect SED changes at all other untrained orientations. We attribute this transfer effect to the relatively broad bandwidth of orientation tuning in the early visual cortex (30–40°). This knowledge is valuable for designing a comprehensive training paradigm that accounts for all orientation channels for treating people with excessive SED, such as amblyopic patients. Furthermore, since early visual cortical information, such as spatial frequency and local motion, is also coded by channels other than orientation channels, a similar consideration should be taken when designing the training stimuli to reduce SED. Such a design principle based on considerations of visual channels can be applied to treat other visual functions in amblyopia (Chung, Li, & Levi, 2006; Huang, Tao, Zhou, & Lu, 2007; Levi & Li, 2009; Levi & Polat, 1996; Li & Levi, 2004; Liu, Zhang, Jia, Wang, & Yu, 2011; Polat, Ma-Naim, Belkin, & Sagi, 2004; Zhou et al., 2008).

Our previous findings suggest that the push–pull training protocol largely affects the interocular inhibitory neural network residing in the primary visual cortex. Since interocular inhibition is an integral part of the binocular visual processing, it is not surprising that the learning gained from the push–pull training protocol extends to other binocular visual functions besides reduced SED. Consistent with this, we have revealed the learning effect extends to binocular rivalry with extended viewing duration and stereo perception (Figs. 8 and 9), both in our current and previous studies. Along this line of thinking, we also predict a reliable correlation exists between these binocular functions and the learning effect. To evaluate this prediction for binocular rivalry, we used our current foveal data and previous parafoveal data (Xu et al., in press), and plotted each observer's predominance ratio (SE/WE) and SED in Fig. 11a. Clearly, these two measurements vary in the same direction ($R^2 = 0.386$, $p < 0.001$). Using the same data, we then obtained the correlation coefficient between the change in the predomi-

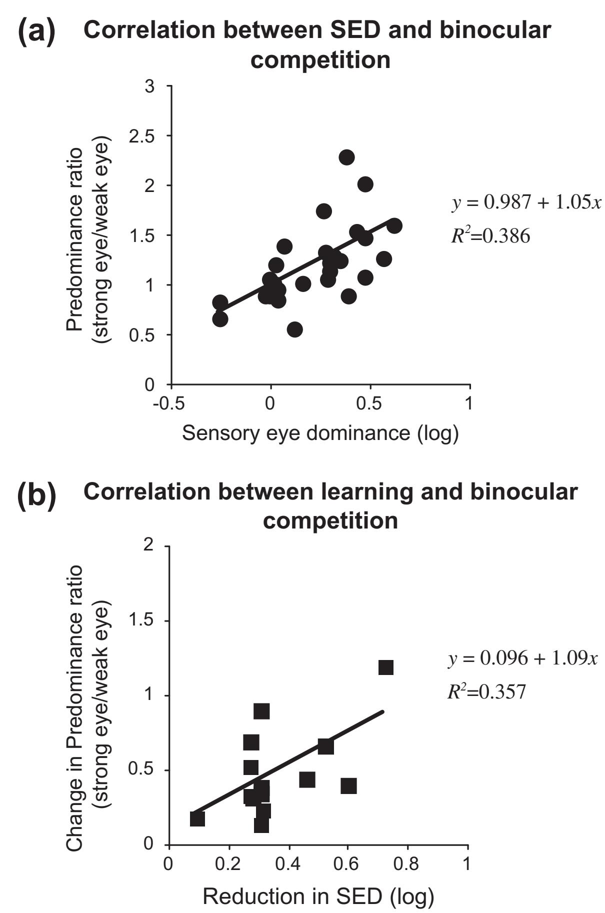

Fig. 11. Correlation between binocular rivalry percepts measured over an extended viewing duration and SED. (a) We correlated the predominance ratio (SE/WE) with SED using data from the current study and those from a previous study (Xu et al., in press). These two measurements vary in the same direction. (b) Using the same data as in (a), we also correlated the change in the predominance ratio (pre–post-training) and the reduction in SED after training. We found a significant correlation, which suggests observers with more reduction in SED have a larger change in the binocular rivalry perception.

nance ratio (pre–post-training) and the reduction in SED after training. As shown in Fig. 11b, we found a significant correlation between these two changes ($R^2 = 0.357$, $p = 0.024$), wherein observers with more reduction in SED have a larger change in their binocular rivalry perception. We also examined the relationship between the reduction in stereo disparity thresholds and reduction in SED (Fig. 12), again using the data from the current experiment and those from Xu et al. (in press). A significant correlation is found ($R^2 = 0.435$, $p = 0.001$), indicating observers whose binocularity became more balanced (reduced SED) also have more reduction in binocular disparity threshold (improved stereoacuity).

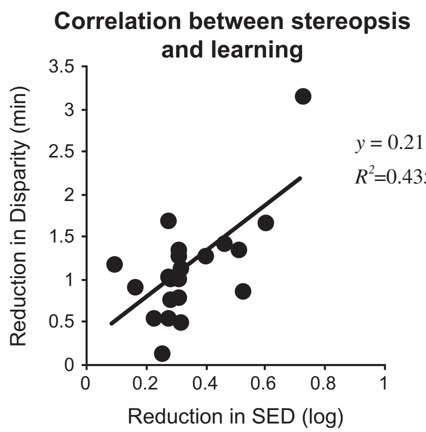

Fig. 12. We plotted the correlation between the reduction in stereo disparity thresholds and reduction in SED, and found a significant correlation. This indicates observers whose binocularity became more balanced (reduced SED) also have more reduction in binocular disparity threshold (improved stereoacuity).

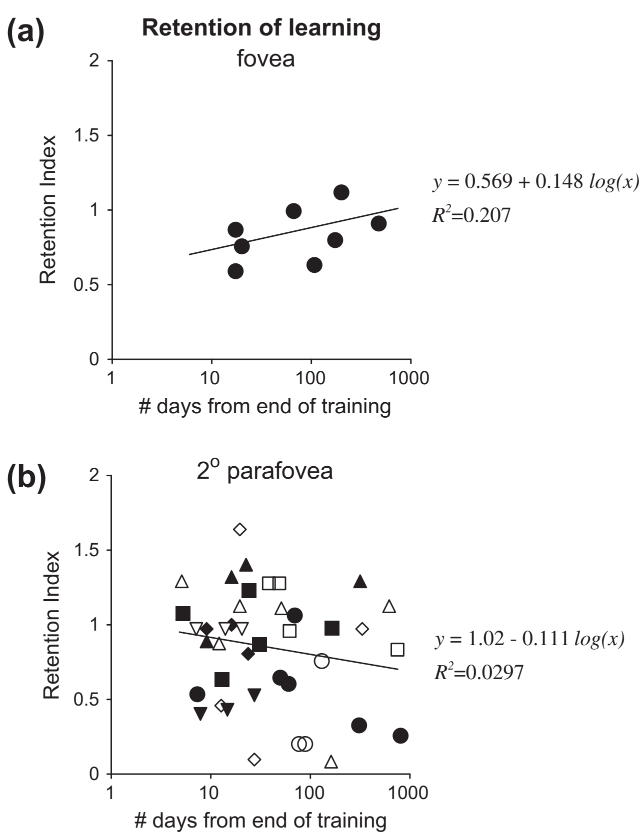

Fig. 13. The retention of learning to reduce SED. (a) The Retention Index (RI) in the fovea of eight observers tested at various days after the training phase ended. (b) The RI at the 2° parafoveal location of ten observers from our earlier study (Xu et al., 2010). Each observer's data are plotted with different symbols and was tested at different days after the completion of training. An RI of unity indicates the learning effect is fully maintained, while an RI of zero indicates the learning effect has dissipated.

Finally, we are encouraged by the possible clinical applications of the push–pull training protocol. We have observed that the learning effect on SED in the foveal (current study) and 2° parafoveal training locations (Xu et al., 2010) can be retained for a relatively long period after the training phase ended, without an intervening re-training session. In the current study, observers returned to the laboratory (each on a different day) for SED testing at the four trained orientations (0°, 45°, 90°, and 135°). The SED data obtained with the four orientations were averaged and used for comparison with the averaged SED immediately after the training terminated. To quantify such a comparison (Fig. 13a) we calculated the Retention Index (RI), which is defined by the following formula:

$$(\mathrm{SED}_{\mathrm{pre}} - \mathrm{SED}_{\mathrm{long\_after}})/(\mathrm{SED}_{\mathrm{pre}} - \mathrm{SED}_{\mathrm{post}}) \qquad (2)$$

In the formula, $\mathrm{SED}_{\mathrm{pre}}$ is the SED measured before the training phase began, $\mathrm{SED}_{\mathrm{post}}$ is the SED measured immediately after the training phase ended and $\mathrm{SED}_{\mathrm{long\_after}}$ is the SED measured some intervals after the training phase ended. Thus, an RI of unity indicates the learning effect is fully retained at the time the $\mathrm{SED}_{\mathrm{long\_after}}$ is conducted, and an RI of zero means the learning effect has dissipated at the time the $\mathrm{SED}_{\mathrm{long\_after}}$ is conducted. Fig. 13a shows that all eight observers' RI (filled circles) is above 0.5, indicating the learning effect at the fovea can be retained for quite a long period. We also analyzed the 2° parafoveal SED data from Xu et al. (2010) in a similar manner and plotted these in Fig. 13b (these data has not been previously reported). Here, each of the ten observers' data points are plotted with different symbols to reflect his/her individual SED changes over the intervals measured (the number of data points are not equal because some observers were able to return to the laboratory more times than others). Overall, all observers' RI are above zero with a mean around unity, indicating the retention of learning.

5. Conclusions

The push–pull training protocol, implemented in the foveal region, significantly reduces SED and improves stereopsis in the foveal region. The push–pull training also significantly changes the dynamics of binocular rivalry by promoting the weak eye's competitive advantage after the training. There exists reliable correlation between these learning effects, suggesting that the push–pull training protocol taps on the interaction between the interocular inhibitory mechanism and the visual processes residing in the primary visual cortex that contributes to these measured percepts. We also observed strong transfer effects of the perceptual learning from the trained orientations and spatial frequency to the untrained ones, when the training stimuli and (untrained) test stimuli are within the same putative bandwidth of the processing channels. The push–pull training can have a long lasting impact on the binocular visual system (reduction of SED and stereo depth threshold), suggesting it leads to rewiring of the visual cortex. This knowledge can be used to guide the selection of a minimal set of training stimuli to efficiently affect all visual channels during the training.

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